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2 Action-matching biases in monkeys (*Sapajus spp.*) in a stimulus-response compatibility task:

3 Evaluating experience-dependent malleability

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Abstract

20 Stimulus-response compatibility effects occur when observing certain stimuli facilitate the
21 performance of a related response and interfere with performing an incompatible or different
22 response. Using stimulus-response action pairings, this phenomenon has been used to study
23 imitation effects in humans, and here we use a similar procedure to examine imitative biases
24 in non-human primates. Eight capuchin monkeys (*Sapajus spp.*) were trained to perform hand
25 and mouth actions in a stimulus-response compatibility task. Monkeys rewarded for
26 performing a compatible action (i.e., using their hand or mouth to perform an action after
27 observing an experimenter use the same effector) performed significantly better than those
28 rewarded for incompatible actions (i.e., performing an action after observing an experimenter
29 use the other effector), suggesting an initial bias for imitative action over an incompatible S-R
30 pairing. After a predetermined number of trials, reward contingencies were reversed; i.e.,
31 monkeys initially rewarded for compatible responses were now rewarded for incompatible
32 responses, and vice versa. In this second training stage no difference in performance was
33 identified between monkeys rewarded for compatible or incompatible actions, suggesting any
34 imitative biases were now absent. In a second experiment, two monkeys learned both
35 compatible and incompatible reward contingencies in a series of learning reversals. Overall, no
36 difference in performance ability could be attributed to the type of rule
37 (compatible/incompatible) being rewarded. Together, these results suggest that monkeys
38 exhibit a weak bias towards action copying, which (in line with findings from humans) can
39 largely be eliminated through counter-imitative experience.

40 *Keywords:* stimulus-response compatibility, imitation, social learning, capuchin monkeys.

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43 Evaluating experience-dependent malleability

44 To imitate, an animal may recreate, through action, the perceived visual qualities of the
45 act they see performed by another. However, the visual information obtained from perceiving
46 another animal's actions often does not correspond to the sensory experience of observing
47 one's own performance of the same action; indeed, sometimes an action is entirely opaque to
48 the actor (e.g., when performing a facial expression). The cognitive challenge in overcoming
49 this so-called correspondence problem (Nehaniv & Dautenhahn, 2002) might explain why
50 researchers examining action imitation (more specifically defined as converting "visual
51 information into matching motor acts", Custance, Whiten, & Fredman, 1999, p. 14), in
52 nonhuman primates, have concluded that there is a qualitative difference in comparison with
53 human abilities (Call & Tomasello, 1995; Fragaszy, Deputte, Cooper, Colbert-White, &
54 Hémery, 2011; Subiaul, 2016; Tennie, Call, & Tomasello, 2012; Tomasello, Davis-Dasilva,
55 Camak, & Bard, 1987). Indeed, the question of imitative ability in animals dates to early work
56 in the comparative tradition (Thorndike, 1911), and has continued in more recent times
57 (Caldwell & Whiten, 2002), however, even those who claim nonhuman apes might possess
58 some capacity to imitate are more cautious when describing the abilities of monkeys (Whiten
59 & van de Waal, in press).

60 Over the last decades, researchers of social learning have documented many failed
61 attempts to observe action imitation in monkeys (e.g., Fragaszy et al., 2011; for reviews see
62 Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 2001), yet studies using simple,
63 extractive foraging tasks have provided some evidence that monkeys will match the body part
64 used by a conspecific to open containers. Voelkl and Huber (2000) found that common
65 marmosets (*Callithrix jacchus*) were more likely to open a box with their hand after observing

66 a conspecific use the same body-part, when compared to individuals who had seen the container
67 opened by mouth. Furthermore, a detailed frame-by-frame analysis of the video footage of
68 these actions found that specific action characteristics measured when the monkeys opened the
69 box with their mouth (e.g., head inclination) were significantly more alike when one monkey
70 had watched another perform the action (in comparison to monkeys who had not observed a
71 conspecific; Voelkl & Huber, 2007). Using a similar methodology with a larger sample of
72 vervet monkeys (*Chlorocebus aethiops*), van de Waal and Whiten (2012) provided further
73 evidence of body-part matching. Subjects were more likely to use their hand after observing a
74 conspecific use that same action when opening a food-baited canister. These studies of bodily
75 imitation in a few species of monkeys provide the extent of positive findings on motor imitation
76 in adult monkeys, although evidence of a distinctive form of imitative behavior, which may be
77 unrelated to the current question of imitation in adult monkeys, has also been reported in
78 neonates (e.g., Ferrari et al., 2006).

79 Developmental approaches to imitation suggest certain types of experience are crucial
80 for imitative ability to develop. For example, the associative sequence learning approach and
81 ideomotor approach posit that imitative ability is formed through compatible sensorimotor
82 experience; i.e., the contingent experience of performing and observing the same action
83 (Heyes, 2010; Heyes & Ray, 2000; Prinz, 1997, 2005). This sensorimotor experience could
84 occur when an infant observes their own actions or by being imitated by caregivers (Del
85 Giudice, Manera, & Keysers, 2009). Support for experiential accounts of imitation has been
86 provided through the use of stimulus-response compatibility (SRC) procedures that incorporate
87 stimulus-response action pairs. With human adults, an action SRC task requires participants to
88 perform two different actions (e.g., hand opening/closing) while simultaneously presented with
89 a task irrelevant image that displays either a compatible action (i.e., the action they must
90 perform) or an incompatible action (i.e., the different action). Reaction times (RTs) are

91 consistently quicker when the image presented corresponds with the action to be performed,
92 while images of incompatible actions invoke slower responses, a phenomenon described as
93 automatic imitation (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, &
94 Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000).
95 This action-specific SRC effect is similar to those found in traditional SRC procedures, where
96 stimuli-response pairs share other overlapping characteristics (e.g., spatial location, Simon &
97 Rudell, 1967; or semantic content, e.g., Stroop, 1935; for a review see Kornblum, Hasbroucq,
98 & Osman, 1990), and has been proposed as a method of studying imitation, mimicry, and
99 mirror neurons in humans (Heyes, 2011).

100 If some forms of imitation are modulated by sensorimotor experience, it follows that
101 these imitation effects are malleable and should be influenced by sensorimotor training; indeed,
102 incompatible training sessions, where participants were required to open their hand after seeing
103 a hand close and vice versa, delivered 24 hours before an action SRC task has been found to
104 significantly reduce compatibility effects in adult humans (Heyes et al., 2005). Catmur et al.
105 (2008) used a similar method to examine activity in brain regions associated with mirror neuron
106 activity, and after incompatible training (performing hand actions when presented with an
107 image of a foot and vice versa), brain areas previously related with hand actions were active
108 when viewing images of a foot, possibly suggesting that the neural substrates thought to
109 facilitate imitative behavior (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Iacoboni et al.,
110 1999), are sensitive to experience. This evidence suggests that existing cognitive relationships
111 between sensory-motor representations, whether innate or learned, are plastic, and can adapt to
112 varied inputs. While a nativist and empiricist approaches to imitation are not necessarily
113 mutually exclusive, a proper understanding of the impact of experience on imitation in

114 nonhuman primates is currently lacking, which presents a stark contrast with the efforts
115 devoted to investigating pre-existing abilities.

116 With human participants, SRC effects identified using action S-R pairings are examined
117 using reaction time measurements. They occur when participants (required to perform specific
118 responses), are unintentionally and automatically influenced by action stimuli in accordance
119 with the compatibility state of the S-R pairing (Brass et al., 2000; Catmur & Heyes, 2011;
120 Stürmer et al., 2000). Compatible S-R pairings therefore typically facilitate performance (fast
121 RTs), whereas incompatible pairings tend to produce interference (slower RTs).

122 Studies that have examined this SRC effect in nonhuman animals follow a different
123 approach (Mui, Haselgrove, Pearce, & Heyes, 2008; Range, Huber, & Heyes, 2011). Instead
124 of examining RT response, subjects are trained to respond with two different actions
125 discriminatively to two action stimuli, and associations between stimuli and responses are
126 learned by trial and error. Learning success is then compared between compatible (i.e.,
127 rewarded for performing the action they see) and incompatible S-R pairings (i.e., rewarded for
128 performing a different action to the one they see), and if compatible pairings are learned more
129 quickly than incompatible pairings, it is inferred that the perceptual qualities of the action
130 stimulus aids in the performance of that same action over a different action, indicative of some
131 imitative ability or bias. Given the training procedure, it is less clear that the compatibility
132 effects can be said to be “automatic” and so the term automatic imitation may be less suited to
133 these findings (although to date, the comparative literature has been described using this same
134 terminology; i.e., Mui et al., 2008; Range et al., 2011).

135 Using this comparative methodology, budgerigars (*Melopsittacus undulates*) rewarded
136 for imitating a conspecific perform a foot versus a beak action have been found to learn the
137 associative rule more quickly than subjects rewarded for performing an opposite action (Mui

138 et al., 2008). Similarly, domestic dogs (*Canis lupus familiaris*) rewarded for opening a door
139 with the same body part as their owner (hand/paw or mouth), learned this rule faster than those
140 rewarded for using the opposite body part (Range et al., 2011). Furthermore, in the study of
141 imitative biases in dogs, it was found that once the animals were reinforced for incompatible
142 rules, their subsequent performance on compatible actions was poorer when compared to dogs
143 that had not experienced incompatible training. The authors concluded that this suggests that
144 previous incompatible experience carried over into the subsequent condition where only
145 imitation was rewarded, which is consistent with experiential accounts of imitative ability. The
146 use of these learning procedures provides a method of assessing whether S-R associations
147 relevant to bodily imitation are facilitated by compatibility effects, thus providing a means by
148 which underlying biases can potentially be revealed.

149 Here, our aims are two-fold. Firstly, using an SRC paradigm, we will examine if
150 capuchin monkeys find compatible S-R actions pairings (i.e., when hand actions are rewarded
151 following presentation of a hand-action stimulus, and mouth actions are rewarded following
152 presentation of a mouth-action stimulus) easier to learn in comparison to incompatible pairings
153 (i.e., when hand actions are rewarded following presentation of a mouth-action stimulus and
154 vice versa). Capuchin monkeys are New World primates that interest researchers of social
155 learning because of their high brain to body-mass ratio (see Fragaszy, Visalberghi, & Fedigan,
156 2004), socially tolerant nature (Fragaszy, Feuerstein, & Mitra, 1997), tool use capacities
157 (Visalberghi, 1993), and evidence of socially learned traditions in wild populations (Perry,
158 2011). Capuchins have been studied extensively to examine their social learning abilities
159 (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009; Fragaszy et al., 2011;
160 Visalberghi & Addessi, 2001) yet no clear evidence of action imitation has been identified in
161 this species (e.g., Fragaszy et al., 2011). However, though previous studies suggest capuchin
162 monkeys learn primarily from non-imitative forms of social learning (Craat, Hardy, &

163 Fragaszy, 2010; Fragaszy et al., 2011; Galloway, Addessi, Fragaszy, & Visalberghi, 2005) the
164 methodology employed here will permit investigation of more subtle imitative biases.
165 Secondly, if imitative biases are present in capuchins we hope to examine whether this bias is
166 resistant to counter-imitative training.

167 In a first experiment we address both of these aims. Capuchin monkeys were rewarded
168 for performing actions with their hand and mouth discriminatively upon observing an
169 experimenter perform hand and mouth actions. Half of the monkeys were reinforced for
170 performing the same action they observed the experimenter perform (i.e., performing hand
171 actions to hand stimuli; mouth actions to mouth stimuli), and the other monkeys were rewarded
172 for performing the alternative action. We predicted that if capuchin monkeys enter into this
173 procedure with some bias to imitate specific motor actions they would perform better when
174 rewarded for the compatible rule. Following this first set of training, the reinforcement of S-R
175 contingencies was reversed; i.e., monkeys that were initially rewarded for compatible
176 responses were rewarded for performing incompatible responses, and vice versa. If capuchin
177 monkeys possess a strong disposition to imitate (whether learned or innate), it might be
178 expected that during this reversal-learning stage those learners switching from an incompatible
179 rule to a compatible rule should perform better than individuals that experience the alternate
180 reversal.

181 **Experiment 1: Two-action stimulus response compatibility task**

182 **Methods**

183 **Subjects and research site**

184 Eight capuchin monkeys (*Sapajus spp.*) were tested in experiment one (six males; mean
185 age at the beginning of the study was 3.9 years, $SD = 2.0$; range = 1.4 - 7.5). All monkeys were

186 housed in one of two mixed-species groups with squirrel monkeys (*Saimiri sciureus*) at the
187 Living Links to Human Evolution Research Centre at Edinburgh Zoo, Scotland. The monkeys
188 were never food- or water-deprived, and all rewards offered during research sessions were
189 supplementary to their diet. Before this experiment took place these capuchins had been studied
190 on a range of cognitive tasks (e.g., Morton, Lee, & Buchanan-Smith, 2013), however, no
191 previous study had examined action imitation. Ethical approval was granted by the University
192 of Stirling Psychology Ethics Committee, and all research took place between February 2011
193 and June 2012.

194 **Materials**

195 Eight research cubicles arranged in a connected 2X4 matrix act as a corridor between
196 the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm X 52.1 cm X 51.4
197 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their
198 groupmates for research purposes. The cubicle window (i.e., the Perspex screen orientated
199 toward the experimenter) included a small opening in its center, allowing juice to be delivered
200 to the capuchins through a mouthpiece connected to a rubber-tube and syringe. On the bottom
201 left side of the cubicle window was a hole (3.5cm diameter) through which food rewards were
202 offered. To shape two disparate actions a modified table tennis paddle was used (see Electronic
203 Supplementary Material, ESM, Video 1.). Alternate sides were colored black and white to
204 facilitate color discrimination training. A second target was used during the stimulus response
205 compatibility (SRC) trials that differed in shape and color (see ESM Video 2). Sessions were
206 recorded on a Sony Mini DV Digital Video Camera.

207 **Shaping behaviors**

208 For monkeys to take part in SRC trials, two actions employing disparate body parts
209 were trained: touching the cubicle window with a) their hand and b) their mouth. These specific

210 actions were used as they were considered similar to those used in previous comparative work
211 (Mui et al., 2008; Range et al., 2011), but also trainable through reinforcement. These actions
212 are not incompatible in the sense of their performance being mutually exclusive (e.g., opening
213 versus closing a hand), but the use of disparate body parts is common practice when studying
214 imitation in primates (e.g., Voelkl & Huber, 2000), as well as stimulus-response compatibility
215 effects in humans and other animals (Catmur & Heyes, 2011; Gillmeister, Catmur, Liepelt,
216 Brass, & Heyes, 2008; Mui et al., 2008; Range et al., 2011). The training of both actions took
217 place concurrently through positive reinforcement of successive approximations of each action.

218 To train each individual to touch the cubicle window with their mouth, diluted fruit
219 juice (one part juice to two parts water) was delivered from a syringe to the mouthpiece on the
220 inside of the cubicle. Capuchins learned to bring their mouths to the screen to receive the juice
221 reward. Next, the experimenter presented the training target ~5cm in front of the window before
222 the juice was delivered. Once capuchins learned to bring their mouths to the window before
223 the juice was delivered, the juice reward was replaced with a food reward. In some instances
224 the monkeys would use their hands to balance themselves against the Perspex screen when
225 performing the mouth action, but this action was still interpreted as a mouth action as the goal
226 was to place their mouth against the screen. To train a distinct hand action the training target
227 was presented to the small hole where food rewards were offered. The target was removed once
228 touched by the subject's hand and a food reward was offered. Gradually, the target was moved
229 further from the hole, and the subject, unable to touch the target directly, was rewarded for
230 touching the window with one or two hands. A monkey was never rewarded for a hand action
231 if their mouth was also presented to the screen. At this point the learned association between
232 stimulus and action was spatial in nature (the mouth action cued by the target presented near

233 the center of the window; the hand action cued by the target presented nearer the left of the
234 window).

235 **Color discrimination learning**

236 Once actions had been shaped and were performed reliably to spatial cues the target
237 was only presented in the center of the window and to be rewarded the capuchin was required
238 to learn a color association rule (see ESM Video 1). The same target (see ESM Video 1) was
239 used to cue both actions, but a different colored side was used in each case (i.e., for four
240 monkeys the black side was always presented when training hand actions and the white side
241 was always presented during the training of mouth actions; the opposite color/action pairing
242 was reinforced for the other four monkeys). Only correct responses were rewarded, i.e.,
243 performing an action that corresponded to a specific color, and if an incorrect response was
244 performed the experimenter turned his back on the monkey for approximately three seconds, a
245 form of negative punishment, removing the opportunity to receive further rewards for a short
246 time-period. Once an individual had performed over 85% correct responses on three
247 consecutive research sessions (20 trials per session), the monkey began the SRC trials.

248 **Stimulus Response Compatibility Trials (SRC)**

249 Upon completion of the color discrimination trials, individuals were transferred into
250 one of two groups: a compatible condition or incompatible condition. During these stimulus
251 response compatibility trials, the color stimulus was switched for an action stimulus (i.e.,
252 instead of seeing a black target or a white target on a given trial, the monkey would see the
253 experimenter touch a target with either his hand or his mouth). Based on performance in the
254 initial color discrimination stage, groups were counterbalanced to include equal numbers of
255 quick discrimination learners (mean number of research sessions before reaching criterion on

256 the color discrimination task was 45.75 for subjects in the compatible condition and 45 for
257 subjects in the incompatible condition). On each research session we attempted to complete
258 twenty SRC trials with each monkey, however, monkeys could end the research session by
259 demonstrating cues to leave and so some sessions included fewer trials. During an SRC trial a
260 second target (see ESM Video 2) was held in front of the experimenter with his left hand and
261 touched with either a) his right hand or b) his mouth. The target was then moved to ~5cm in
262 front of the window. The number of hand and mouth actions performed by the experimenter
263 was kept equal throughout these sessions, i.e., 10 mouth and 10 hand actions, and the order of
264 hand and mouth stimuli was pseudorandomized (the maximum number of repeats was one;
265 e.g., the stimuli performed in half an SRC session might proceed as follows: Hand(H)-
266 Mouth(M)-H-H-M-H-M-M-H-M). Individuals in the compatible condition were rewarded for
267 performing actions using the same body part as the experimenter; i.e., if the experimenter
268 touched the target with his hand, the monkey was rewarded for performing an action with their
269 hand; and if the target was touched by the experimenter's mouth, the monkey was rewarded
270 for using their mouth). Individuals in the incompatible condition were rewarded for using the
271 opposite actions; if the experimenter touched the target with his hand, the monkey was
272 rewarded for performing an action with their mouth, and vice versa.

273 If an action response was ambiguous (i.e., hand placed against the window on its own,
274 and quickly replaced with a mouth response), the target was removed by the experimenter and
275 the trial was repeated. A correct response was rewarded with a food item, and an incorrect
276 response resulted in the experimenter turning his back on the monkey for approximately three
277 seconds. Actions were judged to be correct/incorrect by the experimenter during the research
278 session but all sessions were video recorded for subsequent reliability coding. A random
279 sample of 550 action responses (6%) were extracted from video recordings and information

280 about the action performed by the experimenter (i.e., action stimulus presented) and trial
281 outcome (i.e., whether monkey was rewarded) was removed. These actions were re-coded by
282 the same experimenter that had conducted the experiment, and although this individual was not
283 naïve of the hypotheses, the removal of contextual cues made it impossible to know whether
284 an action performed by a monkey was in response to the same action or a different action.
285 Agreement between the experimenter's decision within the research session and without
286 contextual information was high ($Kappa = .97$; $p < .001$). Once a predetermined learning
287 criterion was reached ($\geq 85\%$ correct responses in three consecutive 20 trial sessions) the reward
288 contingency was to be reversed. However, only one monkey had reached this criterion before
289 900 trials, and due to time constraints, monkeys were switched to the opposite condition
290 regardless of progress after 900 trials, and a further 500 trials were completed by each monkey.
291 Two monkeys were tested on fewer trials in each condition to examine performance on both
292 associate rules without the potential confounding effects of overtraining (320 trials in each
293 condition). As monkeys were free to leave in the middle of sessions and the goal of each session
294 was to test monkeys with 20 trials, monkeys completed on average 10.4 trials more than the
295 established cut-off.

296 It is worth noting that throughout this action stimulus stage we continued to conduct
297 some color discrimination trials to confirm that each subject could still perform both trained
298 actions discriminately. For example, before performing any SRC trials during a given session,
299 four color discrimination trials were completed (color discrimination trials were also performed
300 after the 10th SRC trial and after the 20th trial). We continued to reward this already learned
301 association to encourage participation and to assess an individual's ability to perform both hand
302 and mouth actions discriminately.

303 **Data Analysis**

304 The monkeys' success on each trial was recorded as a binary response variable (either
305 correct or incorrect). This binary variable was used as the outcome variable in a generalized
306 linear mixed model (GLMM) with a binomial distribution and logit link function to test specific
307 hypotheses concerning imitative biases in the SRC paradigm. As each monkey received
308 multiple trials in each condition, the monkey being tested was included as a random intercept
309 in the GLMMs. Furthermore, session number (i.e., consecutive blocks of 20 trials) was
310 included as a random slope in the models. To test hypotheses concerning the persistence of an
311 imitative effect, a model was created with an interaction included for condition and order of
312 learning. To describe the contribution of predictor variables to trial success, odds ratios were
313 calculated by back-transforming the log odds ratios. All statistical tests were conducted with
314 the R statistics program (R Core Team, 2014) in the Rstudio environment (RStudio Team,
315 2014). Models were developed using the lme4 package (Bates, Maechler, Bolker, & Walker,
316 2015), and graphics were created using the ggplot2 package (Wickham, 2009). Monkeys
317 completed up to 900 trials in the first block of learning, but only the first 500 trials for each
318 monkey were examined (320 in the case of two monkeys), for two reasons. Firstly, one
319 monkey's associative rule was switched after 500 trials, so a comparison between groups is
320 balanced at this point (see ESM, Figures 1 and 2 for all performance data summarized for each
321 monkey- areas highlighted in light grey were analyzed). Also, to examine any pre-existing bias
322 in automatic imitative ability it is more appropriate to examine earlier performances.

323 **Results**

324 Overall, monkeys were biased towards mouth actions, performing this action in 54.54%
325 of all analyzed trials. Every monkey developed an effector preference at some stage of the
326 experiment; i.e., the same action was used consistently across a session. For example, when

327 looking at diversity of action performance, we find that across all monkeys and testing sessions,
328 on average, 90.9% of responses within a 20-trial session consisted of one type of action
329 (although this bias could alternate across sessions; e.g., a monkey that performs mainly hand
330 actions in one session might change to mouth responses on the following session). As trial
331 success in this context is unlikely to be related to a learned association between a specific
332 stimulus and response, and as overall success above a 50% chance level requires a diversity of
333 actions, effector was not examined as a predictor of success.

334 Descriptive data on overall performance for each monkey can be found in Table 1 (also
335 see ESM, Figures 1 and 2 for all performance data plotted chronologically by session). A
336 GLMM found a significant interaction between the rule being rewarded
337 (compatible/incompatible) and the order in which the rule was learned (Wald test, β [condition
338 x order] = 0.298, s.e. = 0.148, $z = 2.012$, $p = 0.044$; see Table 2 for full model; see Figure 1). In
339 the first block of discrimination learning the chance of success was significantly lower when
340 learning an incompatible rule (an estimated 22.81% lower odds of being correct, confidence
341 intervals, 95% CIs: 1.33% - 39.62%; Wald test, β [incompatible] = -0.259, s.e. = 0.125, $z = -$
342 2.067, $p = .039$; see Figure 1 when order = first), but in the second block of learning (i.e., after
343 associative rules were switched), the type of associative rule being rewarded did not influence
344 chance of success (Wald test, β [incompatible] = 0.039, s.e. = 0.076, $z = 0.512$, $p = .608$, see
345 Figure 1 when order = second; estimated 3.99% greater odds of success on an incompatible
346 trial, CIs: -10.47% – 20.79%).

347 Discussion

348 When monkeys first learned an association between an action stimulus and an action
349 response, individuals reinforced for a compatible rule performed significantly better than those
350 who were reinforced for an incompatible rule. This finding is the first evidence of a

351 compatibility effect in an action SRC paradigm with nonhuman primates, contributing to
352 existing comparative evidence in birds and dogs (Mui et al., 2008; Range et al., 2011), although
353 it is important to highlight that this initial effect is weak (i.e., estimated CIs = 1.33% - 39.62%),
354 and that only one monkey reached the predetermined learning criterion. The difficulty in
355 learning a compatible action association is consistent with previous work with capuchins that
356 has shown that while certain types of behavior matching is possible (e.g., action that requires
357 the movement of objects), actions themselves are rarely copied (Fragaszy et al., 2011).

358 We found that the marginally superior performance of those rewarded for compatible
359 responses in the first learning block did not persist once reward contingencies were reversed,
360 which suggests that reinforcing certain stimulus-response associations (whether compatible or
361 incompatible S-R associations) subsequently makes it equally difficult to learn the reversed
362 associative rule. The comparable lack of success observed in both conditions in the second
363 block of learning is consistent with predictions of an experience based account of imitation and
364 similar effects observed in humans and other animals (Heyes et al., 2005; Range et al., 2011).
365 However, as only one monkey learned an associative rule (i.e., reaching the predetermined
366 criterion), and as we may have ended training in the second block before a compatibility effect
367 was identifiable we conducted a second experiment to further examine the possibility of a
368 predisposition for imitative ability. In this study we retested two monkeys from experiment one
369 on a series of reversal learning sets to examine if a compatibility bias would be more evident
370 in a repeated reversal design. Using the same SRC procedure used in experiment one, each
371 monkey learned both compatible and incompatible action rules to a predetermined criterion.
372 The small sample used in this second experiment may limit the scope of our conclusions, but
373 if a bias to imitate is present in capuchin monkeys we may expect that following rule reversal,
374 performance on the compatible associative rule would be overall better than on the

375 incompatible rule.

376 **Experiment 2: Repeated reversal learning of a stimulus-response association**

377 **Methods**

378 **Subjects**

379 This second experiment examined repeated reversal learning of compatible and
380 incompatible rules with two male monkeys from experiment one (Chico: 3.4 years and
381 Carlos: 6.2 years at the beginning of experiment 2). These monkeys were selected for this
382 experiment as they were the best learners in the initial learning blocks of their respective
383 conditions (see first block in Table 1). These research sessions took place between October
384 2012 and July 2013, ten months after Carlos' last session in experiment one, and four months
385 after Chico's last session.

386 **Procedure**

387 Both monkeys were tested in a similar fashion to experiment one. In the first block of
388 learning Chico was rewarded for performing incompatible responses and Carlos was rewarded
389 for performing compatible actions. Correct responses were rewarded with a food item and
390 incorrect responses resulted in a three second time-out where the experimenter would turn their
391 back to the monkey. One strategy employed by monkeys in experiment one in an effort to
392 maximize rewards was to perform one action repeatedly (see Results of experiment 1),
393 therefore receiving half of all rewards in each research session. To improve speed of learning
394 and to encourage switching between actions, correctional procedures were introduced. If
395 monkeys responded incorrectly on a trial the same trial was repeated until the monkey either
396 performed the correct response or an incorrect response was performed a certain number of
397 times. We expected that these training procedures would increase the likelihood that a rule will

398 be learned more quickly by forcing monkeys out of single-action biases. Furthermore, we kept
399 these procedures consistent across conditions, so that they would not interfere in interpreting
400 performance. Initially, a trial was repeated up to five times if an incorrect action was performed,
401 however, five consecutive “time-outs” became an overly stringent punishment and subject
402 participation dropped. To increase participation, incorrect responses were instead repeated 3
403 times (this change occurred after 264 trials for Chico, and after 78 trials for Carlos). These
404 incidences were always scored as a single incorrect trial.

405 Learning criterion in this second experiment was altered as it was felt that the initial
406 criterion was unnecessarily strict and may have interfered with the identification of learning in
407 some cases. In the second experiment, to qualify as having learned an associative rule, monkeys
408 had to progress through the following stages. First, a monkey had to provide 65% or more
409 correct responses on a test session consisting of twenty trials. Once this criterion had been met,
410 on subsequent testing sessions monkeys were only tested on ten trial sets. To demonstrate
411 evidence of learning, monkeys had to perform 80% or more correct responses on two
412 consecutive sessions of ten trials (taking place at different testing sessions; i.e., a minimum of
413 an hour between testing). This two-tier criterion was employed as we wanted to offer monkeys
414 sufficient experience of the reward contingencies in the earlier stages of learning. However,
415 we noticed in experiment one that monkeys would sometimes lose interest with the procedure
416 after performing a number of consecutive correct responses (possibly due to satiation). It was
417 predicted that reducing session length to 10 trials during later stages of learning would improve
418 motivation to attend to the procedure and would therefore provide a better measure of learning.
419 Furthermore, this 80% criterion was still highly unlikely to be reached by chance (i.e., 16
420 correct responses in 20 trials is likely to occur by chance only 1.2% of the time), and so, while

421 we believe that reducing the criteria would not have made the rule easier to learn it may have
422 made it easier to identify when a monkey had learned the rule.

423 Once this criterion was met, the associative rule being rewarded was reversed. Over the
424 course of the experiment, Carlos reached the required criterion for the compatible rule three
425 times and the incompatible rule twice, and Chico reached the criterion for both conditions
426 twice. To retain comparable numbers of learning blocks for each monkey, Carlos' first four
427 blocks of learning were analyzed. Throughout these SRC sessions we continued to begin each
428 session with 4 color discrimination trials, to encourage participation and to ensure monkeys
429 could perform both actions discriminately.

430 **Data analyses**

431 The first response to each trial was coded as a binary response variable (correct or
432 incorrect) – correct responses to a repeated trial were not counted. Furthermore, as monkeys
433 reached criterion at different stages for each block of learning we examined the initial
434 performance over the first 60 trials of each learning block. This analysis criteria serves both
435 the function of having a comparable number of trials to compare for both Carlos and Chico
436 (i.e., 240 trials per monkey), and a comparable number of incompatible and compatible trials
437 (i.e., 240 trials per condition). Using a generalized linear model (GLM) with a binomial
438 distribution and logit link function, the effect of condition (compatible/incompatible) and
439 individual subject were examined. This analysis would determine whether an associative rule
440 is easier to switch to after having reached a predetermined number of correct responses on the
441 other associative rule (see above). The interaction between associative rule being rewarded
442 (compatible versus incompatible) and subject was examined to see if performance on
443 conditions was independent of individual monkey.

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Results

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For descriptive data on the number of trials it took each monkey to reach the learning criteria on each learning block see Table 3. A GLM identified a significant interaction between condition and monkey (Wald test, β [monkey x condition] = 1.722, s.e. = 0.392, $z = 4.390$, $p < 0.001$; see Table 4 and Figure 2). There was no difference in performance between conditions for Chico (estimated 15.98% higher odds of success in the incompatible condition, CIs: -32.00% - 97.83%; Wald test, β [incompatible] = 0.148, s.e. = 0.273, $z = 0.544$, $p = 0.586$) and Carlos performed significantly worse on incompatible trials (odds of a correct response were 79.28% lower in the incompatible condition, CIs: 63.97% -88.08%; Wald test, β [incompatible] = -1.574, s.e. = 0.282, $z = -5.576$, $p < 0.001$).

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Discussion

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In this second experiment, further efforts to examine imitative biases in two capuchin monkeys showed no evidence that imitative rules are intrinsically easier than counter-imitative rules over a series of learning reversals sets. As a complement to experiment one we demonstrated that both compatible and incompatible action rules can be learned by two capuchin monkeys, but that overall it is not easier to learn one associative rule over the other. One monkey did perform better when compatible trials were rewarded when compared to incompatible trials, but without further study of a larger sample, we cannot conclusively state whether this finding is driven by an imitation bias, or a bias towards a first-learned association (although, the second monkey in experiment two showed no bias towards either rule).

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General Discussion

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In our first experiment, we report the first evidence from nonhuman primates of an imitative bias in an action stimulus response compatibility (SRC) task. In general, evidence of action imitation in monkeys is scarce, but this result complements evidence of bodily matching

468 reported in New World (Voelkl & Huber, 2000, 2007) and Old World monkeys (van de Waal
469 & Whiten, 2012). It is worth highlighting that only one monkey reached the predetermined
470 criterion in the initial learning block, and that in general, the difficulty that monkeys faced in
471 transferring their previously learned color-action association skills to an action-action
472 associative paradigm demonstrates that this imitative bias is not necessarily automatic in the
473 sense of being reflexive and effortless. At least, the ability to match hand and mouth actions
474 are not readily available to capuchin monkeys (also evidenced by previous research; e.g.,
475 Frigaszy et al., 2011). Indeed, it has been argued that the ability to imitate actions may not be
476 present in any non-human primates (Tennie, Call, & Tomasello, 2009), at least in a manner
477 that does not require considerable training or human enculturation (e.g., Custance, Whiten, &
478 Bard, 1995). Instead, the effect identified here may be an implicit bias that this specific
479 procedure could tap into, and may be related to some other, non-imitative, form of social
480 influence, such as those identified in more naturalistic contexts in primates (e.g., mimicry,
481 response facilitation; Mancini, Ferrari, & Palagi, 2013). Given the many reinforcement trials
482 received across these studies, the difficulty the monkeys faced in reaching the learning criteria
483 in either condition might be puzzling. It is unclear, however, whether this problem stems from
484 an imitative deficiency, or rather a more general problem related to the saliency of action
485 stimuli, or short-term memory capacities for action stimuli. A more general perspective on how
486 imitative learning fits within other domains of social cognition is largely lacking and future
487 work with SRC methods may help understand how imitation fits within this broader context.

488 We recognize that our protocol traded ecological validity for control over stimulus
489 presentation and ease of interpreting action responses, and so future studies may identify
490 stronger imitative effects in more naturalistic contexts (i.e., foraging contexts). Furthermore,
491 the use of a human demonstrator may have influenced attentional or other factors, and although

492 human demonstrators have been used in studies of imitation (Custance et al., 1995; Frigaszy
493 et al., 2011), mirror neurons (Gallese et al., 1996; Keysers et al., 2003), and imitation
494 recognition (Paukner, Suomi, Visalberghi, & Ferrari, 2009), the greater control facilitated by
495 the use of an SRC task may be improved with the use of a conspecific demonstrator. In spite
496 of how these factors were likely to have contributed to the difficulty these monkeys faced when
497 learning this task, we demonstrated that two monkeys were able to meet a strict learning
498 criterion in experiment two. This provided confirmation that, given enough experience,
499 capuchins can learn to distinguish between specific human actions and respond
500 discriminatorily. Indeed, the initial compatibility bias suggests that even in an ecologically
501 artificial set-up, capuchin monkeys must have, to some degree, been sensitive to the
502 correspondence between observed actions and the performance of actions using the same body-
503 part, at least initially.

504 The controlled nature of this method, that incorporated a prolonged testing phase taking
505 place over a number months, allows a more nuanced exploration of action matching when
506 compared with previous efforts with primates (e.g., Voelkl & Huber, 2000; van de Waal &
507 Whiten, 2012) where action matching is assessed from behavior that immediately follows a
508 single observation period (for good reason, as behavior at later stages is confounded by
509 individual learning). We believe that future work incorporating elements of our method, with
510 a wider range of actions and stimulus-response contingencies, could be useful in determining
511 both the action matching abilities of primates and the role of experience.

512 Our findings that an imitative bias is not present following counter-imitative experience
513 (i.e., the second block of reinforcement trials in experiment one and experiment two), suggests
514 that sensorimotor experience can eliminate imitative biases, complementing evidence from a
515 range of other human studies and one finding with dogs (Catmur et al., 2008; Heyes et al.,

516 2005; Range et al., 2011). However, any conclusions concerning a lack of a strong disposition
517 to imitate rests on null findings which must be interpreted with caution (Sainani, 2013).
518 Furthermore, Carlos, one of the two monkeys in experiment two, did perform significantly
519 better when rewarded for compatible responses (see Figure 2), and so it may be that an imitative
520 bias can be maintained in certain contexts. Carlos was the only monkey in experiment one who
521 reached the predetermined learning criterion in the initial learning block, and this initial
522 reinforcement may have led to a persistent advantage for imitative rules across subsequent
523 trials, conducted more than 10 months after this initial reinforcement was received. In contrast,
524 Chico, the monkey who did not display a bias for any particular rule in experiment two, while
525 the best performer in his initial block of incompatible learning in experiment one, did not reach
526 the learning criterion and so was not reinforced preferentially for incompatible response to the
527 same extent as his compatibly reinforced counterpart. This difference in reinforcement history
528 in the first part of experiment one (see Table 1) may explain the individual differences in
529 experiment two, but we stress that this post-hoc interpretation is highly speculative. Overall,
530 the failure to identify strong imitative biases suggests that relationships between sensory and
531 motor representations of actions in monkeys are malleable, at least in some contexts.

532 Given the marginal difference between conditions at the first stage of this experiment,
533 it may not be particularly surprising that initial experience of reinforcement had the effect of
534 minimizing an imitative bias at other stages of this study. However, this effect is notable when
535 considering the persistence of some SRC biases in other domains. For example, one classic
536 study of a traditional stimulus-response compatibility effect (the Simon effect) in adult humans
537 found that compatibility effects were still present in some cases after more than 1500 trials
538 (Fitts & Seeger, 1953), suggesting that when there is strong dimensional overlap in S-R
539 pairings, compatibility effects persist in the face of considerable experience. Of course, there

540 may be greater overlap in the characteristics of some other S-R pairings examined with this
541 procedure (e.g., spatial orientation; Simon & Rudell, 1967). In contrast, and as highlighted
542 earlier, for certain actions (including the mouth action used in this study) the perceptual
543 information available when observing one's own actions and those of another often do not
544 correspond. Instead, in the case of some opaque actions, the associations between stimuli and
545 action responses must be the result of either specific experience linking these (analogous to the
546 learned associations that result in phenomena such as the Stroop effect; Stroop, 1935), or would
547 need to be present from birth in the form of a multimodal matching system (e.g., Meltzoff &
548 Moore, 1997). It should also be emphasized that the absence of an imitative bias following
549 incompatible sensorimotor experience is not irreconcilable with the presence of a multimodal
550 action matching system that exists at birth, as later learning may both inhibit or facilitate a pre-
551 existing imitative bias, and indeed proponents of neonatal imitation accept that later learning
552 is likely to influence imitative ability (Marshall & Meltzoff, 2014).

553 Examples of imitative learning may be rare in capuchin monkeys, but imitation
554 recognition and the role of imitation in facilitating affiliation are also worth considering briefly.
555 For example, capuchins and macaques recognize when the actions of human experimenters
556 correspond to their own and seem to display affiliative behaviors towards these individuals
557 (Paukner et al., 2009; Sclafani, Paukner, Suomi, & Ferrari, 2015). If the mechanism that links
558 observable action to an executed action is forged through associative learning then it is possible
559 that monkeys that have been trained to respond in counter-imitative ways may show increased
560 interest and affiliation towards those that perform contingent non-matching actions. However,
561 if it is discovered that imitation's role in affiliation is still present following incompatible
562 training, then this would call into question the proposal that sensitivity to action matching is
563 purely the result of experience. It may also be the case that the mechanisms underlying

564 imitation's role in learning and affiliation have different origins. Nonetheless, SRC tasks may
565 in the future be a useful tool in examining the link between imitation and affiliation.

566 Overall, this study contributes to a growing understanding of action imitation in
567 primates and the impact of experience on imitative behavior. However, this is only a first step
568 towards understanding the types of experiences that may impact upon imitative ability in
569 primates, and future work is necessary to understand the full extent of experiences' role not
570 only in the elimination of imitative effects, but in the development of these effects. Further
571 work incorporating action SRC paradigms with New and Old World primates may provide
572 unique insight into imitative effects in nonhuman primates, and could be used to test a variety
573 of hypotheses related to the extent and ontogeny of action matching in nonhuman animals in
574 general.

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585 References

- 586 Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models
587 using lme4. *Journal of Statistical Software*, *67*, 1-48. doi:10.18637/jss.v067.i01
- 588 Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement
589 execution in a simple response task. *Acta Psychologica*, *106*, 3–22. doi:10.1016/S0001-
590 6918(00)00024-X
- 591 Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between
592 observed and executed finger movements: comparing symbolic, spatial, and imitative
593 cues. *Brain and Cognition*, *44*, 124–143. doi:10.1006/brcg.2000.1225
- 594 Caldwell, C. A., & Whiten, A. (2002). Evolutionary perspectives on imitation: Is a comparative
595 psychology of social learning possible? *Animal Cognition*, *5*, 193–208. doi:
596 10.1007/s10071-002-0151-x
- 597 Call, J., & Tomasello, M. (1995). Use of social information in the problem solving of
598 orangutans (*Pongo pygmaeus*) and human children (*Homo sapiens*). *Journal of*
599 *Comparative Psychology*, *109*, 308–320. doi: 10.1037/0735-7036.109.3.308
- 600 Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008). Through the
601 looking glass: Counter-mirror activation following incompatible sensorimotor learning.
602 *The European Journal of Neuroscience*, *28*, 1208–1215. doi:10.1111/j.1460-
603 9568.2008.06419.x
- 604 Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and
605 spatial compatibility. *Journal of Experimental Psychology: Human Perception and*
606 *Performance*, *37*, 409–421. doi:10.1037/a0019325

- 607 Crast, J., Hardy, J. M., & Fragaszy, D. (2010). Inducing traditions in captive capuchin monkeys
608 (*Cebus apella*). *Animal Behaviour*, 80, 955–964. doi: 10.1016/j.anbehav.2010.08.023
- 609 Custance, D., Whiten, A., & Bard, K. (1995). Can young chimpanzees (*Pan troglodytes*) imitate
610 arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour*, 132, 837–859.
611 doi:10.1163/156853995X00036
- 612 Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial fruit task in
613 capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 113, 13–23.
614 doi: 10.1037/0735-7036.113.1.13
- 615 Del Giudice, M., Manera, V., & Keysers, C. (2009). Programmed to learn? The ontogeny of
616 mirror neurons. *Developmental Science*, 12, 350–363. doi:10.1111/j.1467-
617 7687.2008.00783.x
- 618 Dindo, M., Thierry, B., & Whiten, A. (2008). Social diffusion of novel foraging methods in
619 brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society of London*
620 *Series B- Biological Sciences*, 275, 187–193. doi:10.1098/rspb.2007.1318
- 621 Dindo, M., Whiten, A., & de Waal, F. B. M. (2009). Social facilitation of exploratory foraging
622 behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology*, 71,
623 419–426. doi:10.1002/ajp.20669
- 624 Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006).
625 Neonatal imitation in rhesus macaques. *PLoS biology*, 4, e302. doi:
626 10.1371/journal.pbio.0040302
- 627 Fitts, P. M., & Seeger, C. M. (1953). S-R compatibility: Spatial characteristics of stimulus and
628 response codes. *Journal of Experimental Psychology*, 46, 199–210. doi:
629 10.1037/h0062827

- 630 Frigaszy, D. M., Deputte, B., Cooper, E. J., Colbert-White, E. N., & Hémary, C. (2011). When
631 and how well can human-socialized capuchins match actions demonstrated by a familiar
632 human? *American Journal of Primatology*, *73*, 643–654. doi:10.1002/ajp.20941
- 633 Frigaszy, D. M., Feuerstein, J. M., & Mitra, D. (1997). Transfers of food from adults to infants
634 in tufted capuchins (*Cebus apella*). *Journal of Comparative Psychology*, *111*, 194–200.
635 doi: 10.1037/0735-7036.111.2.194
- 636 Frigaszy, D. M., & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning &*
637 *Behavior*, *32*, 24–35. doi: 10.3758/BF03196004
- 638 Frigaszy, D. M., Visalberghi, E., & Fedigan, L. (2004). *The Complete Capuchin*. Cambridge,
639 UK: Cambridge University Press.
- 640 Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor
641 cortex. *Brain*, *119*, 593–609. doi:10.1093/brain/119.2.593
- 642 Galloway, A. T., Adessi, E., Frigaszy, D. M., & Visalberghi, E. (2005). Social facilitation of
643 eating familiar food in tufted capuchins (*Cebus apella*): Does it involve behavioral
644 coordination? *International Journal of Primatology*, *26*, 181–189. doi:10.1007/s10764-
645 005-0729-7
- 646 Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based
647 priming of body parts: a study of action imitation. *Brain Research*, *1217*, 157–170.
648 doi:10.1016/j.brainres.2007.12.076
- 649 Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral*
650 *Reviews*, *34*, 575–583. doi:10.1016/j.neubiorev.2009.11.007
- 651 Heyes, C. (2011). Automatic Imitation. *Psychological Bulletin*, *137*, 463–483.
652 doi:10.1037/a0022288

- 653 Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic
654 imitation. *Cognitive Brain Research*, 22, 233–240. doi:
655 10.1016/j.cogbrainres.2004.09.009
- 656 Heyes, C., & Ray, E. (2000). What is the significance of imitation in animals? *Advances in the*
657 *Study of Behavior*, 29, 215–245. doi:10.1016/S0065-3454(08)60106-0
- 658 Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999).
659 Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
660 doi:10.1126/science.286.5449.2526
- 661 Keysers, C., Kohler, E., Umiltà, M. A., Nanetti, L., Fogassi, L., & Gallese, V. (2003).
662 Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, 153,
663 628–636. doi: 10.1007/s00221-003-1603-5
- 664 Kornblum, S., Hasbroucq, T., & Osman, A. (1990). Dimensional overlap: Cognitive basis for
665 stimulus-response compatibility- a model and taxonomy. *Psychological Review*, 97,
666 253–270. doi: 10.1037/0033-295X.97.2.253
- 667 Mancini, G., Ferrari, P. F., & Palagi, E. (2013). In play we trust. Rapid facial mimicry predicts
668 the duration of playful interactions in geladas. *PLoS ONE*, 8, e66481. doi:
669 10.1371/journal.pone.0066481
- 670 Marshall, P. J., & Meltzoff, A. N. (2014). Neural mirroring mechanisms and imitation in human
671 infants. *Philosophical Transactions of the Royal Society of London Series B- Biological*
672 *Sciences*, 369, 20130620. doi:10.1098/rstb.2013.0620
- 673 Meltzoff, A. N., & Moore, M. (1997). Explaining facial imitation: A theoretical model. *Early*
674 *Development and Parenting*, 6, 179–192. doi:10.1002/(SICI)1099-
675 0917(199709/12)6:3/4<179::AID-EDP157>3.0.CO;2-R

- 676 Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias
677 seriously in animal cognition research: a case study in capuchin monkeys (*Sapajus*
678 *apella*). *Animal Cognition*, *16*, 677–684. doi:10.1007/s10071-013-0603-5
- 679 Mui, R., Haselgrove, M., Pearce, J., & Heyes, C. (2008). Automatic imitation in budgerigars.
680 *Proceedings of the Royal Society of London Series B- Biological Sciences*, *275*, 2547–
681 2553. doi:10.1098/rspb.2008.0566
- 682 Nehaniv, C. L., & Dautenhahn, K. (2002). The correspondence problem. In C. L. Nehaniv & K.
683 Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 41–61). Cambridge, MA:
684 MIT Press.
- 685 Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display
686 affiliation towards humans who imitate them. *Science*, *325*, 880–883.
687 doi:10.1126/science.1176269
- 688 Perry, S. (2011). Social traditions and social learning in capuchin monkeys (*Cebus*).
689 *Philosophical Transactions of the Royal Society of London Series B- Biological*
690 *Sciences*, *366*, 988–996. doi:10.1098/rstb.2010.0317
- 691 Prinz, W. (1997). Perception and action planning. *The European Journal of Cognitive*
692 *Psychology*, *9*, 129–154. doi:10.1080/713752551
- 693 Prinz, W. (2005). An ideomotor approach to imitation. In S. Hurley & N. Chater (Eds.),
694 *Perspectives on imitation: From neuroscience to social science: Vol. 1: Mechanisms of*
695 *imitation and imitation in animals* (pp. 141–156). Cambridge, MA: MIT Press.
- 696 R Core Team. (2014). R: A language and environment for statistical computing. [Computer
697 software]. Vienna, Austria: R Foundation for Statistical Computing.
- 698 Range, F., Huber, L., & Heyes, C. (2011). Automatic imitation in dogs. *Proceedings of the*

- 699 *Royal Society of London Series B- Biological Sciences*, 278, 211–217.
700 doi:10.1098/rspb.2010.1142
- 701 RStudio Team. (2014). RStudio: Integrated development environment for R [Computer
702 software]. Boston, MA: RStudio Inc.
- 703 Sainani, K. (2013). Interpreting “null” results. *PM and R*, 5, 520–523. doi:
704 10.1016/j.pmrj.2013.05.003
- 705 Sclafani, V., Paukner, A., Suomi, S. J., & Ferrari, P. F. (2015). Imitation promotes affiliation in
706 infant macaques at risk for impaired social behaviors. *Developmental Science*, 18, 614–
707 621. doi:10.1111/desc.12237
- 708 Simon, J. R., & Rudell, A. P. (1967). Auditory S-R compatibility: the effect of an irrelevant cue
709 on information processing. *The Journal of Applied Psychology*, 51, 300–304. doi:
710 10.1037/h0020586
- 711 Stroop, R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental*
712 *Psychology*, 18, 643–662. doi: 10.1037/h0054651
- 713 Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual
714 gestures and postures: A study of imitation. *Journal of Experimental Psychology:*
715 *Human Perception and Performance*, 26, 1746–1759. doi:10.1037/0096-1523.26.6.1746
- 716 Subiaul, F. (2016). What’s special about human imitation? A comparison with enculturated
717 apes. *Behavioral Sciences*, 6, 13. doi: 10.3390/bs6030013
- 718 Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of
719 cumulative culture. *Philosophical Transactions of the Royal Society of London Series B-*
720 *Biological Sciences*, 364, 2405–2415. doi:10.1098/rstb.2009.0052

- 721 Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes*
722 *schweinfurthii*) fail to imitate novel actions. *PLoS ONE*, 7, e41548. doi:
723 10.1371/journal.pone.0041548
- 724 Thorndike, E. (1911). *Animal Intelligence: Experimental Studies*. New York, NY: Macmillan.
- 725 Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational learning of
726 tool-use by young chimpanzees. *Human Evolution*, 2, 175–183. doi:
727 10.1007/BF02436405
- 728 van de Waal, E., & Whiten, A. (2012). Spontaneous emergence, imitation and spread of
729 alternative foraging techniques among groups of vervet monkeys. *PLoS ONE*, 7,
730 e47008. doi:10.1371/journal.pone.0047008
- 731 Visalberghi, E. (1993). Capuchin monkeys: a window into tool use in apes and humans. In K.
732 Gibson & T. Ingold (Eds.), *Tools, language and cognition in human evolution* (pp. 138–
733 150). Cambridge, UK: Cambridge University Press.
- 734 Visalberghi, E., & Addessi, E. (2001). Social facilitation of eating novel food in tufted capuchin
735 monkeys (*Cebus apella*): Input provided by group members and responses affected in
736 the observer. *Animal Cognition*, 4, 297–303. doi:10.1007/s100710100113
- 737 Visalberghi, E., & Fragaszy, D. M. (2001). “Do monkeys ape?”- Ten years after. In
738 Dautenhahn, L. & Nehaniv, C. (Eds.), *Imitation in animals and artifacts* (pp. 471-499) ,
739 Cambridge, MA: MIT Press.
- 740 Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour*, 60, 195–202.
741 doi:10.1006/anbe.2000.1457
- 742 Voelkl, B., & Huber, L. (2007). Imitation as faithful copying of a novel technique in marmoset
743 monkeys. *PLoS ONE*, 2, e611. doi:10.1371/journal.pone.0000611

744 Wickham, H. (2009). *ggplot2: elegant graphics for data analysis*. New York, NY: Springer-
745 Verlag.

746 Whiten, A., & van de Waal, E. (in press). Social learning, culture and the “socio-cultural brain”
747 of human and non-human primates. *Neuroscience & Biobehavioral Reviews*.
748 doi:10.1016/j.neubiorev.2016.12.018

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763 Table 1.

764 *Descriptive data from stimulus response compatibility (SRC) trials 1-500 for each monkey (320*
 765 *trials for Kato and Sylvie) in both conditions with trial success coded as a binary variable (1*
 766 *represents a successful response and 0 an unsuccessful one). This measure is the equivalent to*
 767 *the proportion of correct responses in a learning block. Standard error of the mean is included*
 768 *in brackets. See Figure 1 for a graphical representation of totals.*

Rule rewarded in 1st Reinforcement Block		Trials per learning block	Mean Trial Success (SE)	
			1st Block	2nd Block
Pedra	Incompatible	500	.506 (.022)	.522 (.022)
Figo	Incompatible	500	.500 (.022)	.478 (.022)
Chico	Incompatible	500	.572 (.022)	.444 (.022)
Kato	Incompatible	320	.500 (.028)	.478 (.028)
Total	Incompatible	1820	.521 (.012)	.481 (.012)
Carlos	Compatible	500	.658 (.021)	.484 (.022)
Micoe	Compatible	500	.562 (.022)	.502 (.022)
Inti	Compatible	500	.516 (.022)	.478 (.022)
Sylvie	Compatible	320	.512 (.027)	.500 (.028)
Total	Compatible	1820	.567 (.012)	.490 (.012)

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773 Table 2.

774 *A Generalised Linear Mixed Model with a binomial error distribution and logit link function*
 775 *is reported below. Trial performance (correct/incorrect) was examined as the dependent*
 776 *variable, and condition (compatible/incompatible) and order of learning (1st block/2nd block)*
 777 *were included as fixed effects. Individual monkey was included as a random intercept in the*
 778 *model and session number was included as a random slope.*

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Random Effects	Variance	STD		
Monkey (intercept)	0.0087	0.0933		
Session	0.0137	0.1169		
Fixed Effects	Estimate	SE	z	p-value
Intercept (Order = First, Condition=				
Compatible)	0.4499	0.1315	3.421	<0.001
Incompatible (when order = First)	-0.2589	0.1253	-2.067	0.039
Order (when condition = Compatible)	-0.5298	0.1366	-3.879	<0.001
Order * Condition	0.2981	0.1481	2.012	0.044

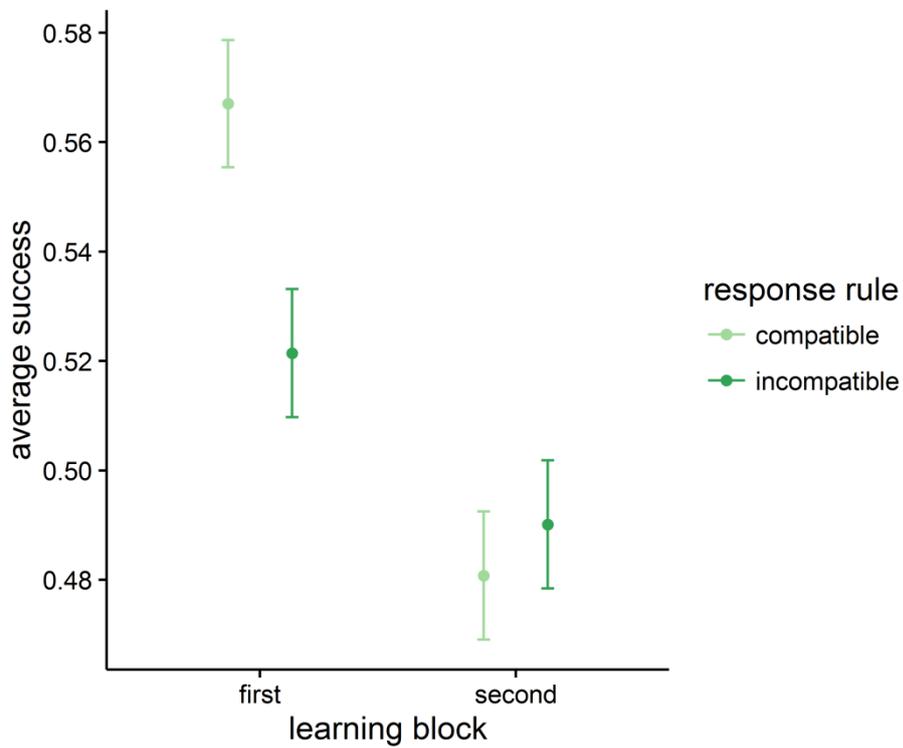
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786 *Figure 1.* Mean proportion of correct responses in the first 500 trials for compatible and
787 incompatible conditions when associative rules are first learned and following rule reversal.

788 Error bars represent standard error of the mean.

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796 Table 3.

797 *Number of trials completed before each monkey reached learning criteria for each learning*
 798 *block. The first letter of the rule learned is in brackets after the trial number (compatible =c;*
 799 *incompatible =i); e.g., Carlos began learning the compatible rule while Chico began with the*
 800 *incompatible rule.*

Number of Trials Before Reaching Criterion

Learning Block	Carlos	Chico	Total
1	200 (c)	204 (i)	404
2	166 (i)	267 (c)	433
3	60 (c)	551 (i)	611
4	280 (i)	541 (c)	821
5	235(c)		
Total	941	1563	2269

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809 Table 4.

810 *To examine whether condition (compatible/incompatible) and monkey (Chico/Carlos)*
 811 *influenced trial success over the first 60 trials of each learning block, we created a*
 812 *Generalised Linear Model with a binomial error distribution and logit link function. The full*
 813 *model is reported below.*

Fixed Effects	Estimate	SE	Z	p-value
Intercept (Monkey = Carlos, Condition=				
Compatible)	0.4754	0.1878	2.532	0.011
Incompatible (when monkey = Carlos)	-1.5740	0.2823	-5.576	<0.001
Chico (when condition = compatible)	-1.2063	0.2706	-4.457	<0.001
Monkey * Condition	1.7223	0.3923	4.390	<0.001

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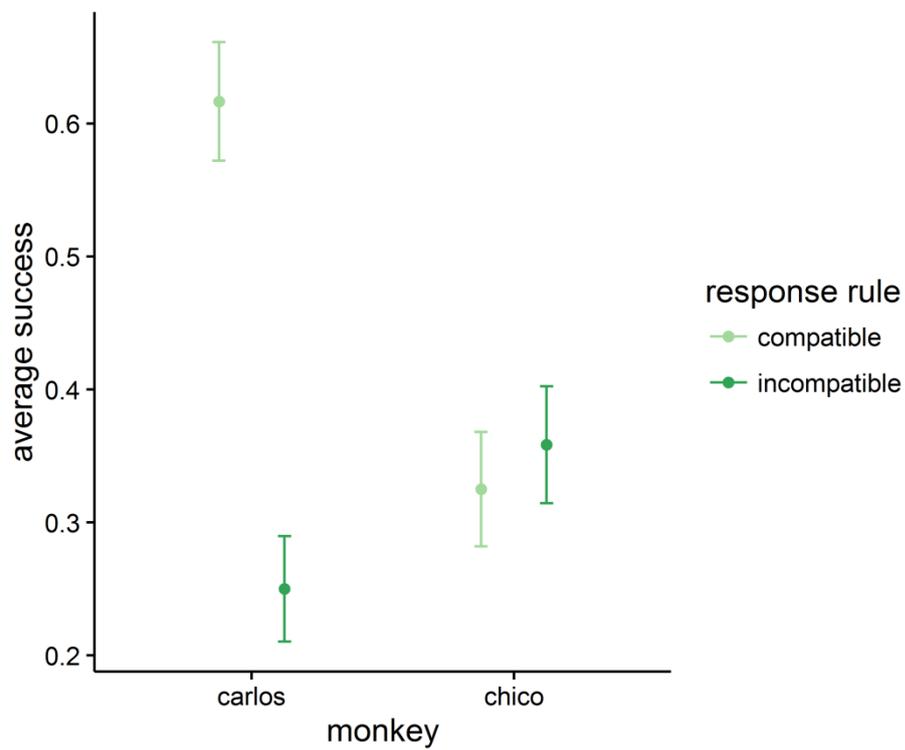
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825 *Figure 2.* Mean proportion of correct responses in experiment two over the first 60 trials of
826 each learning block for both subjects (Carlos/Chico) differentiated by response rule. Error
827 bars represent standard error of the means.

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